SANDAKANIA 6 (1995): 55–62

Notes on a myrmecophytic heterophyllous *Diospyros* (*Ebenaceae*)

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Summary. *Diospyros andamanica* (Ebenaceae), a heterophyllous tree, is documented as a facultative myrmecophyte. Ants of various species build carton structures around clusters of small, cup-shaped leaves and branch bases found along the stem of this tree, and also cultivate scale insects within. It is pointed out that in this species, the availability of suitable nesting space for ants may have been more important than the presence of extrafloral nectaries, found in the form of leaf glands in many species of *Diospyros*, in encouraging a myrmecophytic association.

Although, in the past decade, the biology of ant-plant associations have attracted more interest than previously (see Beattie 1985, Benson 1985, Cutler & Huxley 1991, Keeler 1989), the basic information and lists of Asiatic ant-plants by Bequaert (1922) and Benson (1985) have only been further augmented largely through the recent work of Fiala and Maschwitz and their team based in Southeast Asia (see, for example, Fiala *et al.* 1989, Fiala & Maschwitz 1991, Fiala, Maschwitz & Tho 1991, Maschwitz *et al.* 1989, 1991). The plant species that take part in such myrmecophytic associations come from diverse families, and the ants documented in these associations mostly belong to species of *Camponotus* (including *Colobopsis*), *Cladomyrma*, *Crematogaster Monomorium*, *Nylanderia*, *Tetramorium*, and *Tetraponera* (many Southeast Asian ants cannot as yet be named to species level with confidence).

The associations may be broadly categorised as representing nutrient symbioses, seen primarily in ant-associated epiphytes such as *Hydnophytum* and *Myrmecodia* (Rubiaceae) where ant associates enrich the nutrient status of the plant (Huxley 1978), or as symbioses that afford the plant protection against herbivores or vine-growth, such as in *Macaranga* associations with ants (Fiala, Maschwitz & Tho 1991). Ants inhabit a variety of plant structures in consistent ant-plant associations, usually hollow branch or stem internodes which may be locally swollen (e.g., *Clerodendron fistulosum*, Verbenaceae; *Myrmeconauclea strigosa* and some *Neonauclea* spp., Rubiaceae; *Macaranga constricta*, Euphorbiaceae) or not (e.g., *Millettia nieuwenhuisii*, Papilionaceae; various *Macaranga* spp.), and including inflated stem (hypocotyl) tubers (e.g., *Hydnophytum*, *Myrmecodia*) and hollow rhizomes (e.g., *Lecanopteris*, Polypodiaceae).

Here we report a myrmecophytic association in *Diospyros andamanica* (Ebenaceae), as observed within a population studied on Gemok Hill in eastern Sabah, Malaysian Borneo. This species is heterophyllous, i.e., produces two distinct forms of leaf (see below for details), and has not been documented before as a myrmecophyte. The reason for this most probably is that typically only the non-ant inhabited, more distal flowering portions of the branches are collected as botanical specimens, whereas those parts inhabited by ants (stems near branch bases with small, cup-shaped leaves) were overlooked or ignored.

Architecture and morphology of *Diospyros andamanica*

All trees of *Diospyros andamanica* observed on Gemok Hill in eastern Sabah (vouchers deposited at SAN: SAN 134544 for female tree, SAN 134545 for male tree) were essentially monopodial, with loosely arranged tiers of plagiotropic branches produced at intervals along the stem. Their architecture conforms to Massart's model as elucidated by Hallé, Oldeman & Tomlinson (1978), a model common in the genus. Vertical shoots representing reiterative growth on leaning or damaged stems also show the same growth architecture (Fig. 1).

Trees of this species bear two forms of leaf. Leaves along the plagiotropic branches that are typically large (10–25 cm long), ovate-elliptic, plane and with short but distinct stalks constitute one leaf form (Fig. 2A; also the inflorescences are borne in the axils of such leaves, cf. Fig. 2D). Leaves borne on the stem itself, near the bases of and intermingled with branches, which are small (up to 3.5 cm long at most), broadly ovate to orbicular, with strongly recurved margins making the whole leaf cup-shaped and with scarcely distinct stalks constitute the other leaf form (Fig. 2A–C). On both forms of leaf, there are typically two to four dark, crater-shaped nectariferous glands at the base of the lower surface (Fig. 2D).

Fig. 1. Erect shoot of *Diospyros andamanica*, showing a tier of plagiotropic branches and two forms of leaves. (Photo by C. Puff.)

The ant structures and their inhabitants

Every tree in the population studied harboured ants which built carton structures around the clusters of small, cup-shaped leaves and branch bases along the stem (Fig. 2A–C, Fig. 3). Very often, these carton structures also completely enveloped the stem at these portions, as well as most of the cup-shaped leaves present there (Fig. 3). Within the carton structures were also found brood (although it was not known to which ant species they belonged) and many scale insects (Hemiptera: Coccidae), which were apparently tended by ants.

The identity of ants found in such carton structures from seven different trees is shown in Table 1. These ants are from six species representing five genera in three different families: Dolichoderinae (*Dolichoderus, Technomyrmex*), Formicinae (*Camponotus, Polyrhachis*) and Myrmicinae (*Crematogaster*). The most common was *Crematogaster* sp. A, although it was absent in one of the samples. Two of the samples comprised of one species of ant each, but most samples had at least two species of ant. The fact that several ant species can opportunistically share a nesting space indicates that the

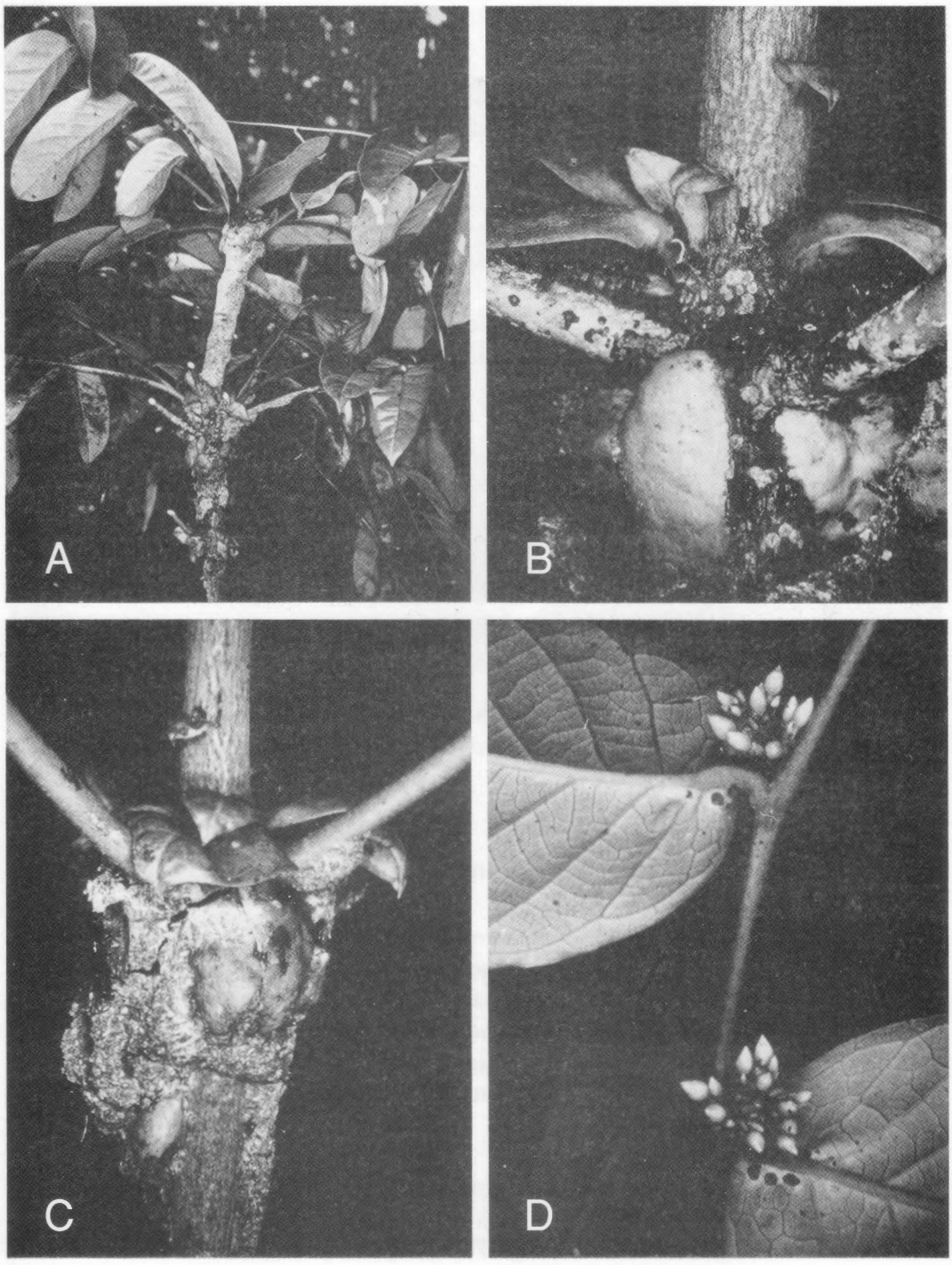

Fig. 2. *Diospyros andamanica.* **A,** shoot with two tiers of branches, and ant carton enveloping the stem. **B,** close-up of space in between small, cup-shaped leaves and branch bases on a stem, showing ants and scale insects. **C,** carton structure built around branch bases and small, cup-shaped leaves on a stem. **D,** lower surface of larger leaves along plagiotropic branches, showing glands at the leaf base and axillary inflorescences. (Photos by C. Puff.)

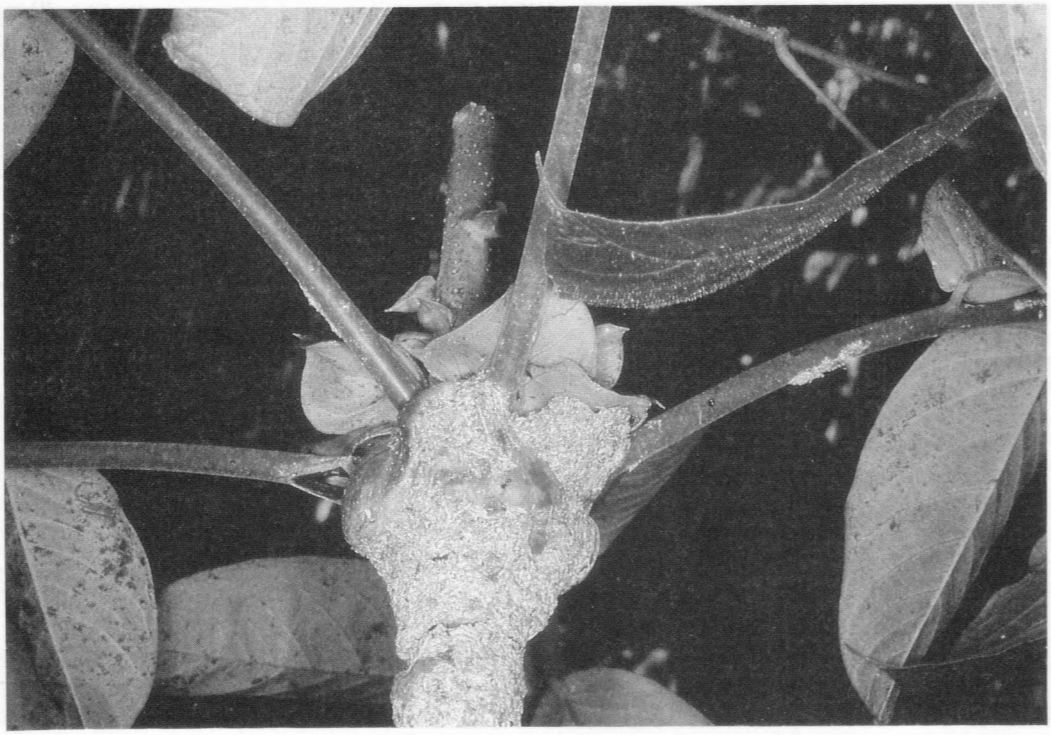

Fig. 3. The ant carton structures in *Diospyros andamanica* often completely envelop the stem as well as branch bases and small, cup-shaped leaves. (Photo by C. Puff.)

association with ants in *Diospyros andamanica* is a facultative one, and not a highly developed obligate association with any one ant.

The relative importance of extrafloral nectaries and available nesting space

In their considerations of the ant-plant relationships shown in *Macaranga* systems, Fiala & Maschwitz (1991) found that the marginal leaf glands of *Macaranga* species that were not obligate myrmecophytes (i.e., not regularly inhabited by ants) functioned as extrafloral nectaries, whereas those of obligately myrmecophytic species secreted a liquid that did not contain any sugar. They noted that some non-myrmecophytic *Macaranga* and a few transitionally myrmecophytic species also had additional extrafloral nectaries on the leaf blade near the leaf stalk insertion. They surmised that reduction of nectary production in ant-inhabited *Macaranga* species was biologically significant as an assimilate-saving device, as these ants also kept scale insects through which they sequestered sugars, and that this lack of extrafloral nectaries helped maintain the specificity of the association through not attracting ants in general. The leaf-base glands of *Diospyros andamanica* in the present case appear to be functional

Table 1. Ants from carton structures collected from seven different trees (T1–7) of *Diospyros andamanica* at Gemok Hill in eastern Sabah. Ant specimens are kept in the spirit collection of the herbarium (SAN) of the Forest Research Centre in Sandakan, Sabah, Malaysia.

Ant family	Ant species	T1	T2	T3	T4	T5	T6	T7
Dolichoderinae	*Dolichoderus sp. A*	+			+			
Dolichoderinae	*Technomyrmex sp.*					+		
Formicinae	*Camponotus sp. A*				+		+	+
Formicinae	*Camponotus sp. B*					+		
Formicinae	*Polyrhachis sp.*			+				
Myrmicinae	*Crematogaster sp. A*		+	+	+	+	+	+

extrafloral nectaries, as they are visited by foraging ants, although scale insects are evidently also cultivated within the carton structures built by ants.

Diospyros is represented by many species in the Bornean lowland forests and many species have distinct glands on their leaves; the fact that obligate myrmecophytism (i.e., specific ant-plant association) appears to be absent in the genus thus far, and that the present case of myrmecophytism is a rare occurrence in the genus and a facultative one involving exploitation of available nesting space by a variety of ant species supports the observation of Fiala & Maschwitz (1991) that the possession of extrafloral nectaries does not appear to have been essential in the evolutionary development of symbiotic ant-plant associations. As also discussed by McKey (1989) and Fiala & Maschwitz (1991, 1992), the provision of suitable nesting space by the plant appears to be fundamentally important in the development of myrmecophytism. In this regard, the heterophyllous condition of *Diospyros andamanica*, an uncommon condition within the genus, may have been important in encouraging a myrmecophytic association.

ACKNOWLEDGEMENTS

We thank Prof. U. Maschwitz and Ms. A. Schellerich of the Zoologisches Institut, J.W. Goethe-Universitat, Frankfurt, Germany, for the ant identifications. Arthur Y.C. Chung kindly commented on a manuscript of this paper. We thank also A. Berhaman, L. Madani and K. Loloh for assistance in the field.

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